Direct and indirect ecosystem responses to vehicle compaction of soft sediments

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Abstract

Change in an ecological community after a disturbance may be a direct impact or may be indirectly mediated through the response of a highly influential species. In northeastern Pacific tidal flats, a native bioturbator, ghost shrimp *Neotrypaea californiensis,* engineers soft-sediment habitat and interacts antagonistically with bivalve shellfish. Vehicle compaction has been used in pest control of ghost shrimp, but this disturbance lacks quantitative evidence of its efficacy and environmental impacts. Through three large (~10 ha) experiments in Grays Harbor, Washington, USA, we tested the direct and indirect impacts of compaction by a tracked vehicle (MarshMaster) on ghost shrimp density, sediment conditions, and infauna. We also examined how oyster survival and waterbird usage of tidal flats responded post-compaction. Compaction pushed <20% of ghost shrimp to the surface, where they were vulnerable to predation and damage, yet did not significantly reduce subsurface densities within 1-2 days. Rather, declines in shrimp density and shifts to smaller size classes appeared at later sample timepoints and were more pronounced with more compaction passes. All compaction experiments resulted in firmer sediment for at least a year, even in the experiment where shrimp densities were unaffected by a single compaction pass. Where compaction briefly reduced shrimp densities below 50 m^{-2}, sediment increased in mud and organic content and infauna increased in abundance, suggesting that these changes were mediated through reduced bioturbation rather than a direct impact of compaction. Similarly, multivariate responses of infauna appeared only in the experiments where compaction reduced shrimp densities. Habitat use by waterbirds was more influenced by tidal stage than by compaction; statistically, only dunlin (*Calidris alpina*) foraged more on compacted than on reference beds. Finally, although survival of outplanted oyster seed improved with compaction at one site, it remained too low (~34-40% yr^{-1}) for viable farming. This implementation of vehicle compaction, with disturbance from as many as five passes or spaced at annual intervals, provided insufficient pest control. Nevertheless, reduced densities of ghost shrimp were associated with follow-on effects on sediment content and the infaunal community.

Introduction

Ecological change following disturbance can be altered by ecosystem engineers (Jones et al. 1994, 1997) as they create habitat and buffer extreme events (Norkko et al. 2002, Harley and O'Riley 2011). When the engineer itself is affected by a disturbance, community-level shifts can occur (Bruno and Bertness 2001). Bioturbation is a major form of ecosystem engineering in soft sediment environments (Reise 2002, Byers and Grabowski 2013). Through sediment ejection, bioturbators can create porous, sandy patches that provide habitat for some infaunal species (Brenchley 1982, Contessa and Bird 2004, Pillay and Branch 2011). Bioirrigation oxygenates deeper sediment, and microtopography created by burrowing or digging contributes to nutrient removal through denitrification, a key ecosystem service (Webb and Eyre 2004, Schenone et al. 2024). At the same time, sediment destabilized or expelled through bioturbation buries organisms at the surface, causing death or emigration of epibenthic species and suspension feeders

(Rhoads and Young 1970, Brenchley 1982, Pillay and Branch 2011). Overall, sediment properties and communities both shift with bioturbation (Posey 1986, Berkenbusch et al. 2000, Pillay et al. 2007b, Volkenborn et al. 2009).

By excluding epibenthic fauna and altering abiotic conditions, bioturbators can be pest species in aquaculture (Nates and Felder 1998, Feldman et al. 2000). In such cases, pest control methods can be considered intentional disturbances that aim to create long-term habitat change through loss of the targeted engineer. Prescribed burns and invasive species removal provide other examples of managed disturbance, although not always generating the intended ecological gains (Penman et al. 2011, Prior et al. 2018). The ecological community could react to the disturbance itself or to the gradual change in physical conditions, mirroring the trajectory of the ecosystem engineer.

In northeast Pacific estuaries, ghost shrimp *Neotrypaea californiensis*, a native bioturbator, conflict with farming of Pacific oysters (*Magallana gigas*), which are commonly grown on-bottom in the region (Feldman et al. 2000, Dumbauld et al. 2001, Ruesink et al. 2025). Axiid ghost shrimp are among the most influential bioturbators in estuarine sediments worldwide, building ephemeral burrows extending up to 1 m deep and expelling 50 g (30 mL) of sediment per shrimp daily (MacGinitie 1934, Dumbauld et al. 2004, Pillay and Branch 2011, Volkenborn et al. 2012, Hull et al. 2025). Low densities of shrimp (>25-50 m^{-2}) bury oysters grown on the sediment surface within a few summer months (Dumbauld et al. 2004, Hull et al. 2025). Maximum shrimp densities can reach 600 m^{-2}, and the shrimp themselves reach total body lengths >10 cm (~18 mm carapace length) (Posey 1986, Dumbauld et al. 1996).

Non-chemical pest control of ghost shrimp is still under development, including a set of methods that alter the sediment, acting as a general disturbance while simultaneously reducing bioturbation (Ruesink et al. 2025). Sediment compaction by driving a tracked vehicle on beds at low tide has been used as a bioturbator control method in oyster aquaculture since the 1960s, and has been increasingly considered as an alternative to pesticide use in Washington state (Ruesink et al. 2025). Despite this history of ghost shrimp management, the effects of vehicle compaction on shrimp densities and soft-sediment ecosystems remain largely unquantified (Ruesink et al. 2025). Vehicle traffic on beaches is known to alter soft sediment macrofaunal communities through direct crushing or burrow destruction, although most studies have focused on areas where driving occurs regularly (Wolcott and Wolcott 1984, Schlacher et al. 2007, MacLeod et al. 2009, Lucrezi et al. 2014) or on trampled paths (Hsu et al. 2009). Vehicle compaction could cause mortality through several mechanisms: organisms could be forced to the surface, where they are vulnerable to predation or damage; harmed through the energetic costs of reburrowing; or immobilized by sediment consolidation and asphyxiated. Timescales of response can be informative. Infaunal communities of mobile species with fast life cycles (e.g. amphipods, polychaetes) typically recover rapidly from fishing- and aquaculture-related disturbances (Kaiser et al. 2006). Organisms with different burrowing methods, i.e. hydrostatic vs. digging with appendages (Dorgan 2015) might have distinct responses to sediment consolidation. Ecosystem responses that are a direct effect of disturbance would be expected at shorter timescales than indirect responses governed by the dynamics of a long-lived, irregularly-recruiting ecosystem engineer.

Vehicle compaction of tidal flats could also influence foraging habitat for waterbirds, which show shifts in distribution and foraging tactics based on prey type, prey availability, and sediment penetrability. Tidal flats are a critical stopover for migrating shorebirds, which forage in both aquaculture areas and ghost shrimp beds (Frazier et al. 2014, Boardman and Ruesink 2023). Some shorebirds will forage in soft mud over harder substrates even when prey density is lower (Kelsey and Hassall 1989), as more penetrable sediments maximize prey accessibility (Myers et al. 1980, Mouritsen and Jensen 1992, Kuwae et al. 2010). At the same time, high densities of bioturbators can deter foraging if the bioturbator is not itself a preferred prey (Palomo et al. 2003), complicating predictions of shorebird response. It is unclear whether vehicle compaction would alter sediments or infaunal communities enough to influence birds foraging in spring, many months after the compaction event.

Ecological responses to vehicle compaction could derive directly from the disturbance or indirectly from a shift in the density of the dominant ecosystem engineer. These mechanisms are often challenging to distinguish since a disturbance may be required to remove axiid shrimp (Skilleter et al. 2005, Contessa and Bird 2004; but see Pillay et al. 2007). In the context of aquaculture, farmers and managers must understand both the efficacy and non-target effects of pest control methods to decide on best practices for a region (Cahill et al. 2022).

We aimed to test the effects of vehicle compaction and compaction intensity on ghost shrimp and associated physical and community-level responses. We specifically addressed treatment effects on ghost shrimp density and size frequency distribution, sediment penetrability, mud and organic content, infaunal abundance, and multivariate community structure. We also evaluated the post-compaction response of outplanted oysters and bird use of tidal flats during spring migration. We used the timing of changes to infer mechanisms by which compaction could influence these responses, including direct damage due to compaction or lagged effects associated with changes in sediment consolidation or reduced ghost shrimp densities.

Methods

Study sites. Grays Harbor is a 20,000 hectare west-opening estuary located in southwestern Washington State, USA, characterized by extensive tidal flats surrounding a central dredged shipping channel. Our experimental sites were located 8 km north of the mouth of the bay, at Damon Point (46.99°N, 124.13°W), and 3.2 km south, at Westport (46.89°N, 124.09°W; Supplemental Figure S1). Both sites are sandy intertidal flats; Damon Point had more gravel and fine sediment in addition to sand (Table 1). Our experiments took place on bivalve culture beds that were abandoned in 2018 after shrimp densities increased. Shrimp at Damon Point colonized former clam and oyster beds (K. Deerkop, pers. comm.). At Westport, shrimp moved downslope into existing oyster beds (G. Ruggles, pers. comm.).

Experiment 1 - Annual compaction treatment. At Damon Point, the total area was divided into five beds, each covering about 2 ha (Fig. 1, Supplemental Fig. S1). The beds were arranged along an intertidal contour (0.2-0.6 m relative to mean lower low water [MLLW]), and the second and fourth compacted using a tracked MarshMaster MM 2LX (ground pressure 1 psi; Supplemental Fig. S2A) on 12-13 August 2022 and 18-19 May 2023. Compaction consisted of a single pass of the MarshMaster, except one bed was compacted on two successive days in August 2022. Vehicle tracks overlapped so that each round compacted the gap between the tracks on the previous round to ensure all ground was covered. Sampling – detailed in sections below – occurred seasonally (late winter, summer, early fall) over three years, including 1-2 days after compaction (Supplemental Fig. S3), with usually six subsamples per bed.

Experiment 2 – Single pass compaction treatment. At Westport, the total area was divided into five beds, each covering about 2 ha (Fig. 1, Supplemental Fig. S1). The beds were arranged along an intertidal contour (0.4 m MLLW), and the second and fourth compacted on 2 August 2023. Sampling occurred seasonally for a year, including 1-2 days after compaction, with six subsamples per bed.

Experiment 3 – Gradient of compaction. At Westport, nine 0.16 ha beds were established above the single-pass beds for an experiment testing repeated compaction that began on 24 July 2024 (“Westport Multiple”; Fig. 1, Supplemental Fig. S1). Three beds were uncompacted. In between these were beds in a gradient of 1, 3, and 5 passes. The MarshMaster drove over all these beds once, then repeated two more passes on the 3x and 5x pass treatments, and finally made two more passes on the 5-pass treatment bed. Overall, reference beds (0x) were replicated three times and 1x, 3x and 5x pass treatments were replicated twice. Shrimp brought to the surface by the MarshMaster were counted in 1 m^2 quadrats 30 minutes to 1 hour after the vehicle had completed treatment (6-10 subsamples per bed). Any shrimp within 2 cm of the surface were categorized by size class. Thereafter, sampling occurred seasonally, including 1-2 days after compaction (Supplemental Fig. S3), with four subsamples per bed.

Table 1. Characteristics of study sites before compaction. Mean (SE) [N]. N = total number of samples at the study site prior to compaction.

	Experiment 1 Damon Point (Aug 2022)	Experiment 2 Westport Single (Aug 2023)	Experiment 3 Westport Multiple (Jul 2024)
Geolocation	46.996°N, 124.132°W	46.892°N, 124.088°W	46.893°N, 124.089°W
Mud content (%)	3.27 (0.51) [16]	1.20 (0.17) [30]	0.39 (0.03) [11]
Gravel content (%)	0.41 (0.35) [16]	0.01 (0.01) [30]	0 (0) [11]
Organic content (%)	1.33 (0.09) [16]	1.34 (0.04) [30]	1.09 (0.04) [11]
Penetrability (depth in cm)	113.5 (3.2) [16]	134.5 (2.5) [30]	140.0 (2.3) [6]
Shrimp density (m^{-2})	110.0 (17.1) [16]	224.0 (31.2) [30]	352.0 (21.1) [6]

Shrimp. For each subsample on a bed, shrimp were sampled with quintuplet cores to 70 cm within 1 m^2 (Fig. 1). Cores were collected with a clam gun (stainless steel, 12.8 cm diameter and 36 cm length with 50-cm handle), inserted twice to reach the target depth of 70 cm. Sediment was released from the core onto a fabric mat, where it was sorted by hand for shrimp. Adult ghost shrimp are obvious due to their bright orange coloration. Each subsample (= five cores) covered a surface area of 0.0625 m^2 and volume of 0.044 m^3. Shrimp were tallied by size into five size classes by carapace length (CL): recruits <4 mm, extra small 4-8.28 mm, small 8.29-12.49 mm, medium 12.5-17.42 mm, and large >17.42 mm. The recruit size corresponds to shrimp <1 year old, whereas larger sizes cannot be reliably used to assign age (Bosley and Dumbauld 2011). Recruits were not included in analyses or visualizations as they can be easily missed and are unlikely to contribute substantially to bioturbation. The total (less recruits) within each 5-core sample (0.0625 m^2) was multiplied by 16 to give shrimp m^{-2} for visualizations. Statistical analyses were run on the original field counts.

Surface sediment collection and measurement of sediment penetrability. Sediment sampling was carried out concurrently at the same stations as shrimp sampling (Fig. 1, timeline in Supplemental Fig. S3). Sediment (30 mL) was collected with a syringe corer to a depth of 5.4 cm. Organic content was determined using the loss-on-ignition method. Sediment was dried at 45°C for at least 72 hours, homogenized and weighed, held in a furnace at 500°C for 3 hours, and reweighed, to determine dry mass and organic content. Ashed sediment was dry-sieved through a sieve series (Wentworth scale, 63 micrometers to 2000 micrometers) on a sieve shaker (Ro-Tap, W.S. Tyler, Mentor, OH, USA). Sediment smaller than 63 micrometers was classed as “mud” (silt and clay). Sediment penetrability was measured using a penetrometer (Supplemental Fig. S2B), a device consisting of a 159 cm tall metal rod with a movable 2.25 kg weight encircling an additional section of rod between two plates. For each subsample, the rod was placed vertically on the mudflat, the weight was dropped 3 times, and the distance measured from the plate to the sediment. The final measurement was subtracted from 159 to give the depth of penetration into the sediment in centimeters, a measure of bed softness.

Infauna. Infauna were collected for all subsamples using a core (10 cm depth, 10 cm diameter, 785 cm^3) and separated from fine sediment in the field using a 500 micrometer sieve. Samples were preserved in 95% ethanol within 4 hours of collection. Under a dissecting scope, fauna were identified to the best practical taxonomic resolution (generally family for polychaetes, species for amphipods and bivalves, and order for other taxa) and counted, discarding headless individuals and any individuals too damaged to identify. Total counts were summed individuals per core, excluding meiofauna (nematodes, foraminifera, copepods) that were unlikely to be fully sampled by the 500-micrometer mesh size.

Oyster survival and growth. Survival of ground cultured oysters was determined at Damon Point and Westport Single by tethering seeded cultch at six stations on each bed. Seeded cultch are individual valves of large oysters on which juvenile oysters (spat) have settled in a hatchery. Each piece of cultch had a hole drilled through it, which was used to tether the shell to a PVC pole (Supplemental Fig. S2C). Cultch were outplanted at Damon Point on 17 August 2022 (10 cultch at each of six stations per bed) and collected 17 May 2023. A new set of cultch was outplanted at Damon Point on 1 August 2023 (ten cultch at each of six stations per bed), and two per station were collected on 14 September 2023, 29 March 2024, 8 July 2024, and 17 September 2024. Cultch were outplanted at Westport Single on 2 August 2023 (six cultch at each of six stations per bed), and two per station were collected on 17 August 2023, 28 March 2024, and 19 September 2024. The initial average number and height of live spat was recorded from a random subset of the seeded cultch before outplanting. Each collected cultch was examined for live and dead oysters, and up to nine live oysters measured. Spat were counted as living if the animal was still able to hold its valves closed. Live oysters were measured for shell height in mm (umbo to lip).

A commercial operator planted 1 ha of seeded cultch on one of the compacted beds at Damon Point on 22 July 2023. Quadrats (0.25 m^2, 8-40 samples) within this area were recorded for density of cultch on 1 August 2023, 14 September 2023, 30 March 2024, 8 July 2024, and thereafter for density of clusters, since one cluster develops per cultch, on 17 September 2024, 4 April 2025, and 16 June 2025.

Bird usage of tidal flats. At Damon Point, bird habitat usage was measured using time-lapse photography on six daylight tides in spring 2023 (April 10-12, 24-26) and seven in spring 2024 (April 1-3, 11-12, 15-16) (Fig. 1). Birds on the beds were counted over the course of a low tide, using cameras (GoPro Hero 3+ Silver Edition) deployed before the ebb and retrieved after the flood. Photographs were taken every two minutes from 1 m above the sediment, with the interval set by a CamDo intervalometer. A bamboo stake was placed 7 m from the camera to show field of view and to define tidal stage timing. Ebb was defined as the time at which the water's edge passed the camera (when the frame appeared fully dry), and flood as the time at which it passed the bamboo stake (when the frame was fully flooded). Low water was defined as the timepoint halfway between the ebb and flood. The tidal stages were divided into six periods: 24-10 minutes before the ebb, 8 minutes before to 6 minutes after the ebb, 8-22 minutes after the ebb, 16 minutes around low water, 24-10 minutes before the flood, and 8 minutes before to 6 minutes after the flood. Birds were identified and counted in these photographs and summed within stages. All cameras were placed at a similar tidal elevation across beds, moved daily, and faced away from the sun (northeast to northwest depending on time of day). We avoided sloughs when making observations, and fields of view did not overlap.

Data analysis. All analyses were done in R (v.4.5.1, R Core Team 2025). Generalized linear mixed effects models (GLMMs) were built using the package glmmTMB (v.1.1.8, Brooks et al. 2017) and residuals checked with DHARMa (v.0.4.6, Hartig 2022). For the two Westport experiments, samples were collected five times over a year, including 1-2 days post-compaction (Immediate), and each timepoint was analyzed separately to clarify the timing of any treatment effects. At Damon Point, samples were collected over three years and were grouped to examine patterns at different intervals, specifically 1-2 days post-compaction, 1-9 months after the first and before the second compaction event, one year following the second compaction, and in the third year of the study. Additionally, March and early April samples of 2023-2025 were grouped as “Winter” due to low detectability and activity of shrimp during this season (Dumbauld et al. 1996).

Univariate responses: Shrimp, sediment, infauna. Six univariate variables were tested for response to compaction: shrimp counts, shrimp size structure, sediment penetrability, mud content, organic content, and total infauna counts. For the Damon Point and Westport Single experiments, response variables were compared between compacted and reference, with a random intercept to account for the nested design of multiple subsamples per bed. For the gradient of compaction intensity in the Westport Multiple experiment, the number of passes (0, 1, 3, 5) was considered a continuous predictor variable in analyses; bed was included as a random intercept. If the compaction treatment proved significant in these time-specific analyses of shrimp density or sediment penetrability, we followed up by analyzing the combined data over time to test for recovery, that is, significant treatment x time (continuous) interactions. Immediate (within 2 days) and Winter samples were excluded from this recovery analysis for shrimp counts due to their distinct patterns.

Data distributions in these analyses are reported in Supplemental Tables 1-3. All count data were analyzed assuming a generalized poisson distribution, or poisson (moving in some cases to gaussian or lognormal) if that improved residuals. Sediment properties were assumed to follow a gaussian distribution, changing to lognormal if residuals were improved. Shrimp size analyses considered shrimp in two size categories: small + extra-small (4 mm < CL < 12.5 mm) and large + medium (CL ≥12.5 mm). Counts in these two categories were used as a response variable, assuming binomial data distribution.

Infauna multivariate analysis. For infauna composition, all visualizations and analyses used the vegan package (v.2.6-4, Oksanen et al. 2022). Rare species (appearing in <5% of samples) were removed, along with meiofauna and insects. Cores were averaged by bed to avoid pseudoreplication, each taxon was relativized by maximum abundance to give a value between 0 and 1, and a distance matrix was calculated using the Bray-Curtis method. We used a permutational analysis of variance with treatment (compacted vs. reference for Damon Point and Westport Single, continuous for Westport Multiple) and days since compaction (categorical) as explanatory factors, plus the interaction. Differences between treatments and dates were visualized using non-metric multidimensional scaling. If compaction altered community composition, an indicator species analysis was performed with the *multipatt* function in the indicspecies package (De Cáceres and Legendre 2009) to determine particular taxa associated with each treatment.

Oyster survival. Oyster survival was examined over time by analyzing the counts of oysters on cultch outplanted to compacted and reference beds, which occurred at Damon Point and Westport Single. Counts of live oysters per cultch were used as response variables in GLMMs, compaction treatment was a fixed effect, and time (continuous) and the interaction (treatment x time) were included for deployments where cultch were collected repeatedly. Bed was a random intercept. When subsamples consisted of multiple cultch collected from a station at one time, their counts were averaged and rounded to the nearest integer for analysis. For the hectare of commercially-planted oysters, we simply report oyster cultch (cluster) density over time.

Bird usage of tidal flats. For GLMMs applied to birds, tidal stage and treatment were included as main effects, and date (categorical) and bed were included as random effects. Low tide was set as the reference level for tidal stage, and ebb and flood periods were compared to low tide. To prevent singular convergence, no interaction effect was included in bird models. The three most common waterbirds, gulls (*Larus* spp.), dowitchers (*Limnodromus* spp.), and dunlin (*Calidris alpina*), were analyzed separately;

other birds, such as crows and yellowlegs, were rare. No dowitchers were spotted during the low on any date. GLMMs cannot accurately model variance for groups composed only of zeros, so one dowitcher was added to a single randomly selected low to allow the model to run.

Results

Ghost shrimp were pushed to the surface during vehicle compaction, where we observed them to reburrow if they were not eaten by birds (seagulls, pelicans) or damaged by the tracks on the MarshMaster. Surfaced shrimp were only quantified at Westport Multiple, where they were always <20% of endobenthic densities (1x pass: 15 m^{-2}; 3x pass: 50 m^{-2}; 5x pass: 36 m^{-2} at the surface compared to 352 m^{-2} in reference cores; Table 1), and also relatively large (1x pass: 94%, 3x pass: 85%, 5x pass: 72% in medium and large size classes compared to 59% in reference cores).

Shrimp. There were no immediate shrimp density responses to compaction in any of the experiments; shrimp were cored up live and were not detectably reduced by compaction within 1-2 days (Fig. 2A, 3A, 4A, Supplemental Tables S1, S2, S3). The longer-term effects differed by experiment. At Damon Point, one or two compaction passes reduced shrimp densities by 74% relative to reference beds at the 1-9 month period (Fig. 2A), whereas shrimp densities did not respond to one compaction pass at Westport Single during the same timeframe (Fig. 3A). We note a statistically significant difference in shrimp densities between compacted and reference beds at Westport Single at the 1-year sample but cannot attribute this to compaction because the lag seems too long. When the Westport site was compacted with a gradient of passes, up to 5x, shrimp densities responded after two weeks, with more passes causing larger shrimp reductions (to 63% lower density, Fig. 4A). Because of the overall higher densities of shrimp at Westport than Damon Point, even the 5x treatment at Westport did not reduce shrimp below the reference density at Damon Point; that is, shrimp densities on compacted beds were still high despite being reduced from ambient at Westport Multiple. Following the second compaction at Damon Point in May 2023, shrimp continued to occur at reduced density on compacted vs. reference beds, and this pattern persisted into the third year of the study. Treatment differences were evident in winter samples despite the low detectability of shrimp at Damon Point (Fig. 2A, Supplemental Table S1). In the two experiments where compaction reduced shrimp density, recovery was evident over time (treatment x time interaction $P<0.001$ at Damon Point and $P=0.06$ at Westport Multiple; Supplemental Table S4, Fig. 2A, 4A).

Shrimp were smaller in size on compacted than reference beds at Damon Point and at Westport Multiple (Fig. 2B, 4B, Supplemental Tables S1, S3). At Westport Multiple, these smaller size classes became increasingly represented over time in beds with more passes. No consistent shift in size structure occurred at Westport Single where densities never diverged (Fig. 3B, Supplemental Table S2).

Sediment and penetrability. Penetrability immediately decreased on all compacted beds at all sites, usually by ~0.5 m (Fig. 2C, 3C, 4C, Supplemental Tables S1, S2, S3). Compacted beds remained firmer than reference beds over the full study period in all three experiments, regardless of whether shrimp densities were affected. At Damon Point, compacted beds were significantly firmer than reference beds from immediately after the initial compaction event (August 2022) to the final timepoint (June 2025; Fig. 2C). For Westport Multiple, sediment penetrability decreased as number of passes increased, with 5x beds being the most firm following compaction (Fig. 4C). Even in the absence of shrimp reductions at Westport Single, penetrability showed a significant effect, in which compacted beds were less penetrable than reference beds for a year (Fig. 3C). Nevertheless, all compacted beds became more penetrable over time, and the differences between penetrability of compacted and reference beds declined (Supplemental Table S5).

Mud and organic content only changed in treatments where large reductions in shrimp densities occurred. At Damon Point, compacted beds showed increased mud and organic content in sediment 10 months after the first compaction (one month after the second), which persisted through the end of the study (Fig. 2D,E, Supplemental Table S1). Westport Single, where shrimp densities were unaffected, showed no effect of compaction on mud or organic content (Fig. 3D,E, Supplemental Table S2). Generally, in the year after the gradient of compaction at Westport Multiple, sediment properties did not change consistently; significant timepoints showed more mud and less organic content with compaction intensity (Fig. 4D,E, Supplemental Table S3).

Infauna. In total, we identified 31,708 individuals from 20 polychaete families, 11 bivalve species, 19 arthropod taxa, and members of 4 other phyla in the three experiments. Compaction did not reduce infaunal densities immediately in any experiment (Fig. 2F, 3F, 4F, Supplemental Tables S1, S2, S3). At Damon Point, at all later time periods, infaunal densities were substantially higher on compacted than reference beds (Fig. 2F). No treatment differences in infaunal density occurred at Westport Single between two weeks and one year post-compaction (Fig. 3F). The gradient of compaction at Westport Multiple showed statistically-elevated infaunal densities only at eight weeks (Fig. 4F

These infaunal abundance patterns were mirrored by community composition, which differed by treatment at Damon Point and Westport Multiple although the contribution of treatment to total variation was small (r^2=0.05-0.06, Fig. 5, Supplemental Table S6). For subsets of the data from Damon Point, where nine post-compaction timepoints were sampled, infauna did not differ by treatment in August and September 2022 (2 and 43 days post-compaction; r^2=0.053, pseudo-F=0.45, P=0.88), but tended to be distinct the following summer (June and September 2023; r^2=0.25, pseudo-F=2.7, P=0.051) and certainly in summer 2024 (July and September 2024: r^2=0.28, pseudo-F=3.13, P=0.01). From indicator species analysis, *Monocorophium* spp. (amphipods) were significantly associated with compaction, and the polychaete group Paraonidae was significantly associated with reference beds. The indicator species analysis at Westport Multiple showed that Platyhelminthes were associated with the 3x treatment, whereas *Urothoe* spp. (amphipods) disappeared from the 5x treatment. At Westport Single, compaction had no significant effect on macrofauna either initially or over a year (Figure 5, Supplemental Table S6). Macrofauna communities at all sites shifted over time, with winter often in a distinct section of multivariate space on the NMDS plot (Fig. 5).

Oyster survival and growth. Oyster survival was improved by compaction at Damon Point (Fig. 6, Supplemental Table S7). From an initial density of 14 per valve (SE = 2.3, N=20) in August 2022 to collection on 18 May 2023, compacted beds decreased to an average of 7.1 (SE = 0.46) surviving spat per valve, compared to 5.15 (SE = 0.38) for reference beds. From August 2023 to September 2024, oysters declined steadily from a pre-outplant average of 7 spat per valve (SE = 0.73) to 2.15 spat per valve (SE = 0.39) on compacted beds and 0.07 spat per valve (SE = 0.046) on reference beds. The significant treatment x time interaction reflected that oyster survival was overall higher on compacted beds and decreased slower than on reference beds. Surviving oysters on compacted beds had a final average height of 86.9 mm (SE = 1.94) compared to 38.4 (SE = 15.8) for reference beds. At Westport Single, survival averaged <50% across all beds within the first several months, and cultch was visibly buried by 17 August 2023. The number of living spat decreased significantly by date with no effect of treatment (Fig. 6, Supplemental Table S7). By the final collection, only one subsample still had living oysters.

Within the 1 ha area of commercial cultch planted on a compacted bed at Damon Point, cultch (and then cluster) density declined from 22 m^{-2} (SE=6.3, N=13 quadrats) in August 2023 to 3.3 m^{-2} (SE=0.8, N=18) in July 2024 and stabilized at 2.2 m^{-2} in April and June 2025 (April SE=0.1, N=41; June SE=0.6, N=34)

(Supplemental Figure S4). By the end of the study, many of the oysters were only visible as shell lips, with the rest under the sediment.

Bird usage of tidal flats. All three common waterbird taxa at Damon Point exhibited tide-following behavior, as evident by main effects of some tidal stages relative to the low (Fig. 7, Supplemental Table S8). Dunlins followed the ebb tide and returned with the flood, mostly disappearing from the surveyed area during the low. Gulls were more abundant during the ebb than at the low, reappearing immediately before and during the flood. Dowitchers were more abundant during any tidal stage when the water level was nearby, with no birds seen at low tide when the bed had been dry for at least an hour (Supplemental Table S8). Dunlins were the only birds that responded significantly to compaction, appearing in greater numbers on compacted beds (Fig. 7, Supplemental Table S8).

Discussion

The three farm-scale compaction experiments in this study demonstrate that vehicle compaction immediately firms sediment, can result in ghost shrimp declines after a few days, and can lead to accumulation of mud and organics, as well as a shift in infaunal communities (Fig. 2-5). These sediment and infaunal responses are consistent with reduced bioturbation, rather than compaction per se, as they occurred only in experiments where shrimp declined; that is, the non-target effects directly due to disturbance appeared small. Responses were stronger with repeated compaction and lasted at least 1-2 years. Overall, disturbance from vehicle compaction caused both direct environmental responses and indirect change mediated through altered ecosystem engineering by *N. californiensis*. However, this level of surface compaction did not reduce ghost shrimp sufficiently to meet commercial aquaculture needs for pest control (Fig. 6).

Vehicle compaction creates low to moderate reduction in ghost shrimp density if repeated

Ghost shrimp densities did not consistently decline after 1-2 vehicle compaction passes, while repeated compaction was more effective (Fig. 2A, 3A, 4A). Our results support the idea that ghost shrimp are protected by their deep burrows from disturbance at the surface. Generally, burrowing organisms are in little danger from surface pressure. While crustaceans can be crushed during surface sojourns (Wolcott and Wolcott 1984, Schlacher et al. 2007), *N. californiensis* rarely comes above-ground (Stevens 1929). Crushing shrimp is not a viable mechanism for control, given the few shrimp expelled from their burrows by one pass and damaged by the next, as seen by the absence of an immediate compaction effect. The small fraction of ghost shrimp pushed to the surface (<20%) and timing of density declines (lagged by days) both suggest that compaction led to delayed mortality below-ground, consistent with sub-surface immobilization. *N. californiensis* individuals can survive over 100 hours in anoxic conditions (Thompson and Pritchard 1969), but will eventually asphyxiate if unable to move to ventilate their surroundings. While the magnitude of the compaction effect increased with number of passes, the 5x beds still only showed a 63% reduction in shrimp density.

Shrimp showed recovery trends over the 1-2 years of post-compaction sampling (Fig. 2A, 3A, 4A, Supplemental Table S4). In principle, ghost shrimp populations could recover by recruitment or by migration from adjacent beds. The post-compaction change towards smaller shrimp indicates that these were more resistant to sediment consolidation, and recovery occurred through recruitment rather than lateral movement (Fig. 2B, 3B, 4B). *N. californiensis* has a wide-ranging pelagic larval stage, with no strong link between recruitment and adult abundance within a bay (Dumbauld et al. 1996). Reducing adult ghost shrimp therefore should not alter the number of larvae arriving in autumn from the coastal ocean, which would then contribute smaller individuals to the recovering populations.

Compaction directly changes penetrability; other sediment properties respond with a lag

Vehicle compaction consistently created firmer sediment, even when it failed to reduce shrimp densities (Fig. 2C, 3C, 4C). Where bioturbation creates loose-packed sediment, even the relatively light downward pressure exerted by the MarshMaster firmed the beds. The sediment remained firm in compacted areas at all three experiments by the final sampling (1-2 years after the most recent compaction); shrimp remaining on these beds were ejecting sediment and sorting particles without returning penetrability to reference levels. This duration of firmer sediment was longer than might be expected from short-term shrimp removal, in which porosity and particle size distribution track ghost shrimp recovery (Contessa and Bird 2004).

The timing of mud and organic accumulation aligns with the idea that ghost shrimp rather than compaction affects sediment composition. Compacted beds at Damon Point became distinguishable from reference beds only in the summer following compaction, when calmer conditions allowed fine sediment to settle out of the water (Fig. 2D,E). No sediment change occurred at Westport Single, where shrimp densities were unaffected by compaction (Fig. 3D,E). On compacted beds with lower shrimp densities, less resuspension and erosion leads to accumulation of mud particles relative to areas of high shrimp activity, while less deposit feeding is occurring that would reduce organic content. Greater sediment stability can foster growth of bacteria and microalgae, while bioturbation can reduce biofilms through burial and erosion (Webb and Eyre 2004, Pillay et al. 2007b, Thomas et al. 2024, Volkenborn et al. 2009).

Macrofaunal communities change when compaction reduces ghost shrimp

In association with reduced density of *N. californiensis* at Damon Point and Westport Multiple, infauna communities differed between compacted and reference beds (Fig. 5), and infaunal abundances diverged over time at Damon Point (Fig. 2F). Few taxa were identified through Indicator Species Analysis to be diagnostic of treatments. Among these, Corophiid amphipods are known to be harmed by pesticides used against ghost shrimp, yet rapidly reach higher densities once ghost shrimp have been controlled (Dumbauld et al. 2001). Conversely, the amphipod genus *Urothoe* (not in 5x treatment), is associated with deep-burrowing organisms, including Japanese ghost shrimp *Neotrypaea harmandi* (Tamaki et al. 2018). While frequent trips by vehicles (multiple per day) reduce abundance and diversity within the resulting tracks on tidal flats (MacLeod et al. 2009), our sites did not diverge within the first several weeks, as would be expected if ground pressure altered communities. Where shrimp densities were statistically unaffected at Westport Single, we observed no community change on compacted beds despite firmer sediment. Infaunal samples at Westport Multiple were collected two weeks to one year after compaction and showed a statistical response to compaction intensity in multivariate analyses (Fig. 5C) without substantial increases in infaunal densities (Fig. 4F). Across all experiments, vehicle compaction itself did not kill off infaunal species, nor did infauna respond only to a change in penetrability.

The altered infaunal community on compacted beds at Damon Point persisted for two years following the second round of compaction. Natural loss of ghost shrimp allows competitive inferiors to expand into former shrimp beds in a process that takes years, assuming annual recruitment and limited adult mobility (Takeuchi et al. 2013). Our data were not sufficiently resolved to address any lags in the reverse process, that is, return of a shrimp-associated infaunal community as shrimp recover. However, the strong patterns of temporal change at all sites are consistent with a dynamic infaunal community that would keep pace with shifts in bioturbation.

Waterbird usage is mostly tide-driven

Waterbird abundance was mostly linked to tidal stage rather than compaction, with all three focal species following the tide. Numerous studies support the idea that birds prefer to forage along the water’s edge, where the sediment is relatively soft and prey activity is high (Kuwae et al. 2010, Miller and de Rivera 2014, Ponsero et al. 2016). Compared to the strong influence of tidal stage, waterbirds were mostly unaffected by compaction. Gulls and dowitchers continued to forage equally on compacted and reference beds. Dunlin, the smallest focal species, were slightly more abundant on compacted beds. The high prey abundance on compacted beds may have compensated for the difficulty of foraging in firmer sediment. While greater penetrability normally increases prey accessibility (Myers et al. 1980, Mouritsen and Jensen 1992, Kuwae et al. 2010), birds will forage on firm sediment if prey availability is high (Rosa et al. 2007), and dunlin may have responded to the higher total abundance of shallow infauna on compacted beds. In general, unstructured tidal flats, regardless of ghost shrimp density, may be equivalent habitat for birds. A study of habitat use in Oregon found that birds used *N. californiensis*-dominated sandflats much as other habitats (Frazier et al. 2014). Above-ground structure added with shellfish culture can alter shorebird foraging, in a manner specific to gear type and bird species (Burger and Niles 2017, Boardman and Ruesink 2023).

Epibenthic shellfish still excluded

In our study, compaction as a disturbance did not shift the system sufficiently to create an ecological opening for oysters, the inferior antagonist, to survive long-term. A critical threshold for oysters on sediment occurs at about 25 shrimp m^{-2}, above which they are smothered with sediment (Dumbauld et al. 2004, Hull et al. 2025). On working farms in Washington State, seed oyster survival on-bottom reaches 70% annually (Ruesink et al. 2023) or 80% through the summer months of greatest shrimp activity (Hull et al. 2025), whereas survival on compacted beds in the current study was substantially lower (Fig. 7). Firmer sediment, which was seen in all compacted areas, did not in and of itself keep oysters at the surface. This was evident with the near-total mortality of the Westport Single outplants. Oyster mortality is likely caused by burial due to ejected sediment (Hull et al. 2025) rather than sinking on more penetrable beds.

Management implications

This study showed that repeated compaction by vehicles on a tidal flat could reduce ghost shrimp densities. Yet, even multiple compaction passes did not reduce ghost shrimp densities enough to allow ground culture of oysters, although also appearing to have limited direct non-target effects. Due to the wide dispersal of ghost shrimp larvae, any control method will have to be applied to aquaculture beds every several years, as pesticides were (Feldman et al. 2000, Dumbauld et al. 2006). Driving on beds during the crop cycle, which typically lasts three years, would likely cause oyster mortality. While a vehicle with higher ground pressure might more effectively immobilize shrimp underground, it would have a high risk of becoming stuck on these soft intertidal flats.

Management of ghost shrimp on shellfish beds is unlikely to be achieved through vehicle compaction alone, and the large-scale collaborative experiments reported here bring closure to decades of attempts to use vehicle compaction as a stand-alone control method for shrimp. Looking ahead, shellfish growers will likely continue to use a variety of bed-working techniques, from harrowing to dredging to layering beds with shell or gravel, to “harden” ground and create optimal conditions for their crops. The “roller-chopper” attachment for the MarshMaster only reaches 30 cm into the sediment, which may explain why its impacts are not notably greater than vehicle compaction (Ruesink et al. 2025). Permeable barriers or mats used against bioturbators in other systems (Volkenborn et al. 2007) might serve if the mesh size were small (1 mm); larger mesh mats and thin (<10 cm) layers of shell or gravel have not been effective (Ruesink et al. 2025). As clarified by the current study, hardening without reducing shrimp densities still allows sediment ejection that buries ground-cultured oysters. The evidence of lagged mortality, in which shrimp die due to immobilization rather than damage from surface pressure, opens up potential new avenues for technical solutions that better destroy burrows and pack sediment around shrimp underground. Altered farming techniques are also being explored, including off-bottom methods that can be accessed by boat to avoid dangerous sediment conditions; floating culture is globally well-established as a culture method for oysters. In a more dynamic farming strategy, natural shifts in ghost shrimp distribution may free up some areas for culture as other areas need to be abandoned. These alternatives require capital outlay or substantial acreage and are not suitable for all farms, supporting the need for continued research to improve effectiveness of mechanical control of ghost shrimp.

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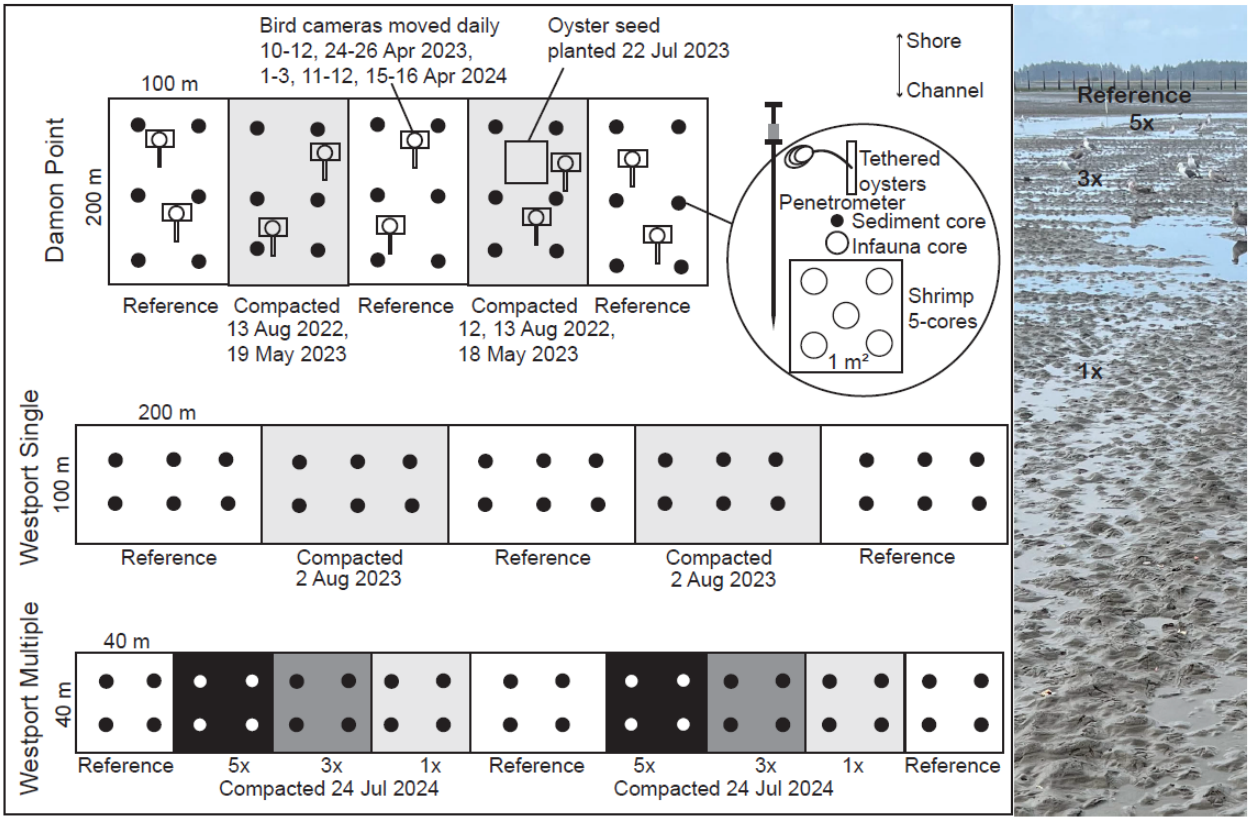

Figure 1. Experimental design testing vehicle compaction of intertidal flats in Grays Harbor, Washington (USA) in three experiments where sediment and faunal responses were measured. At Damon Point, 2-ha beds were compacted once or twice initially in Aug 2022 and again in May 2023, and compacted and reference beds were followed through June 2025. At Westport, 2-ha beds were compacted once in Aug 2023 and, along with reference beds, followed for a year. Due to minimal treatment effects at this site, a second experiment was set up on 0.16-ha beds that were compacted with 0, 1, 3, or 5 passes in Jul 2024 and followed for a year (Westport Multiple). The plots in all experiments were established along an elevation contour: 0.2-0.6 m relative to mean lower low water at Damon Point, 0.4-0.5 m MLLW for Westport Single, and 0.6 m MLLW for Westport Multiple. Photograph is from 25 Jul 2024 looking along contour of treatment plots at Westport Multiple, showing rapid burrow reconstruction. Geolocations are in Table 1, sites are mapped in Supplemental Figure S1, and data collection timepoints are specified in Supplemental Figure S3.

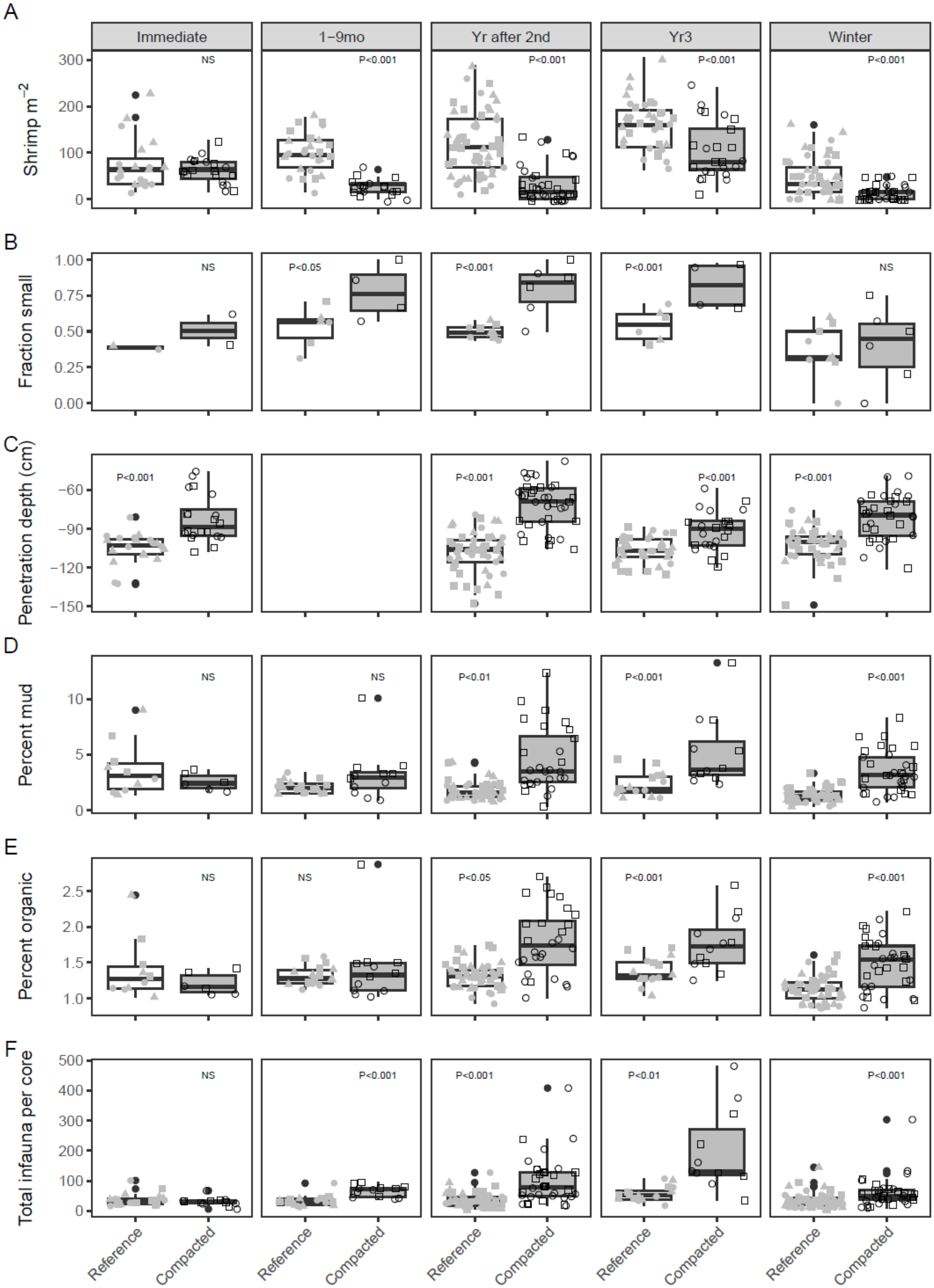
A
Immediate
1–9mo
Yr after 2nd
Yr3
Winter
Shrimp m^{-2}
300
200
100
0
NS
P<0.001
P<0.001
P<0.001
P<0.001
B
Fraction small
1.00
0.75
0.50
0.25
0.00
NS
P<0.05
P<0.001
P<0.001
NS
C
Penetration depth (cm)
-60
-90
-120
-150
P<0.001
P<0.001
P<0.001
P<0.001
D
Percent mud
10
5
0
NS
NS
P<0.01
P<0.001
P<0.001
E
Percent organic
2.5
2.0
1.5
1.0
NS
NS
P<0.05
P<0.001
P<0.001
F
Total infauna per core
500
400
300
200
100
0
NS
P<0.001
P<0.001
P<0.01
P<0.001
Reference
Compacted
Reference
Compacted
Reference
Compacted
Reference
Compacted
Reference
Compacted

Figure 2. Responses to compaction of intertidal flats at Damon Point (Grays Harbor), Washington (USA) over three years, with timepoints binned. A) Density of ghost shrimp *Neotrypaea californiensis* from core samples. B) Fraction of 1+-year old shrimp in small or extra-small size classes (>4 - <12.5 mm CL). C) Depth of penetration of a standard metal rod (negative is further into the ground). D) Percent mud (grain size <63 μm) in mineral sediment. E) Percent organic in dry sediment. F) Macro-infauna counts per core (diameter 10 cm, depth 10 cm). Immediate samples were on 14 Aug 2022, one day after initial compaction was complete. The 1-9 month samples were collected in Sep 2022 and May 2023. Samples from the year after the second compaction were collected in Jun and Sep 2023 and Jul 2024. Yr3 samples were collected in Sep 2024 and Jun 2025. Samples collected in late Mar or early Apr of 2023-2025 are grouped as “Winter”. Sampling occurred on two (2-ha) compacted beds interspersed between three reference beds; in the graphs, all subsamples from a bed share a point symbol. Boxplots are based on subsamples for visualization, but statistical analyses appropriately accounted for the nested design and true replicates of two compacted and three reference beds.

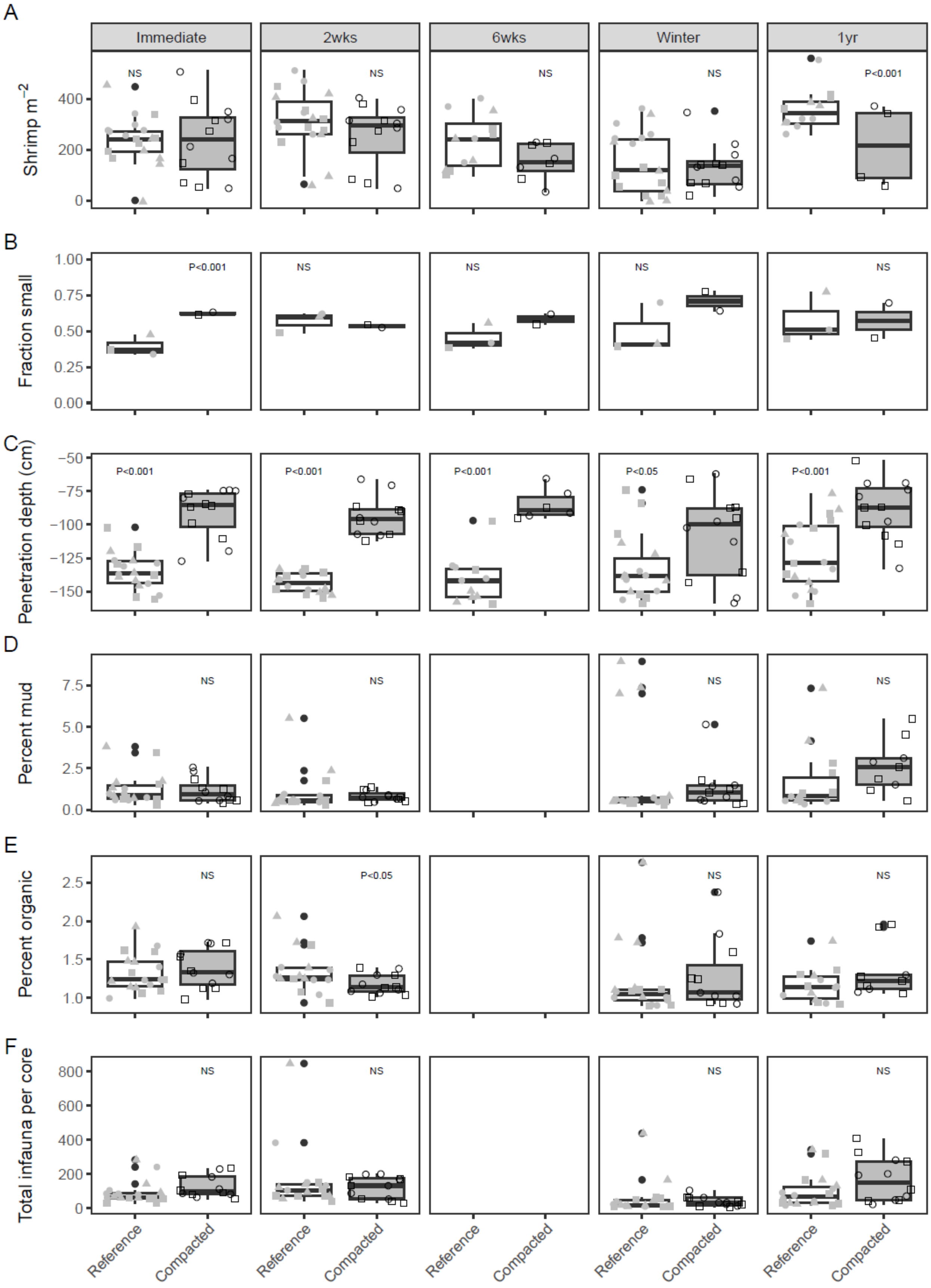
A
B
C
D
E
F
Immediate
2wks
6wks
Winter
1yr
Shrimp m^{-2}
Fraction small
Penetration depth (cm)
Percent mud
Percent organic
Total infauna per core
NS
P<0.001
P<0.05
0
200
400
0.00
0.25
0.50
0.75
1.00
-50
-75
-100
-125
-150
0.0
2.5
5.0
7.5
1.0
1.5
2.0
2.5
0
200
400
600
800
Reference
Compacted

Figure 3. Responses to compaction of intertidal flats at Westport (Grays Harbor), Washington (USA) over one year following a single compaction pass. A) Density of ghost shrimp *Neotrypaea californiensis* from core samples. B) Fraction of 1+-year old shrimp in small or extra-small size classes (>4 - <12.5 mm CL). C) Depth of penetration of a standard metal rod (negative is further into the ground). D) Percent mud (grain size <63 μm) in mineral sediment. E) Percent organic in dry sediment. F) Macro-infauna counts per core (diameter 10 cm, depth 10 cm). Immediate samples were on 2 Aug 2023, one day after compaction was complete, and each additional faceted column is a subsequent sample timepoint. Sampling occurred on two (2-ha) compacted beds interspersed between three reference beds; in the graphs, all subsamples from a bed share a point symbol. Boxplots are based on subsamples for visualization, but statistical analyses appropriately accounted for the nested design and true replicates of two compacted and three reference beds.

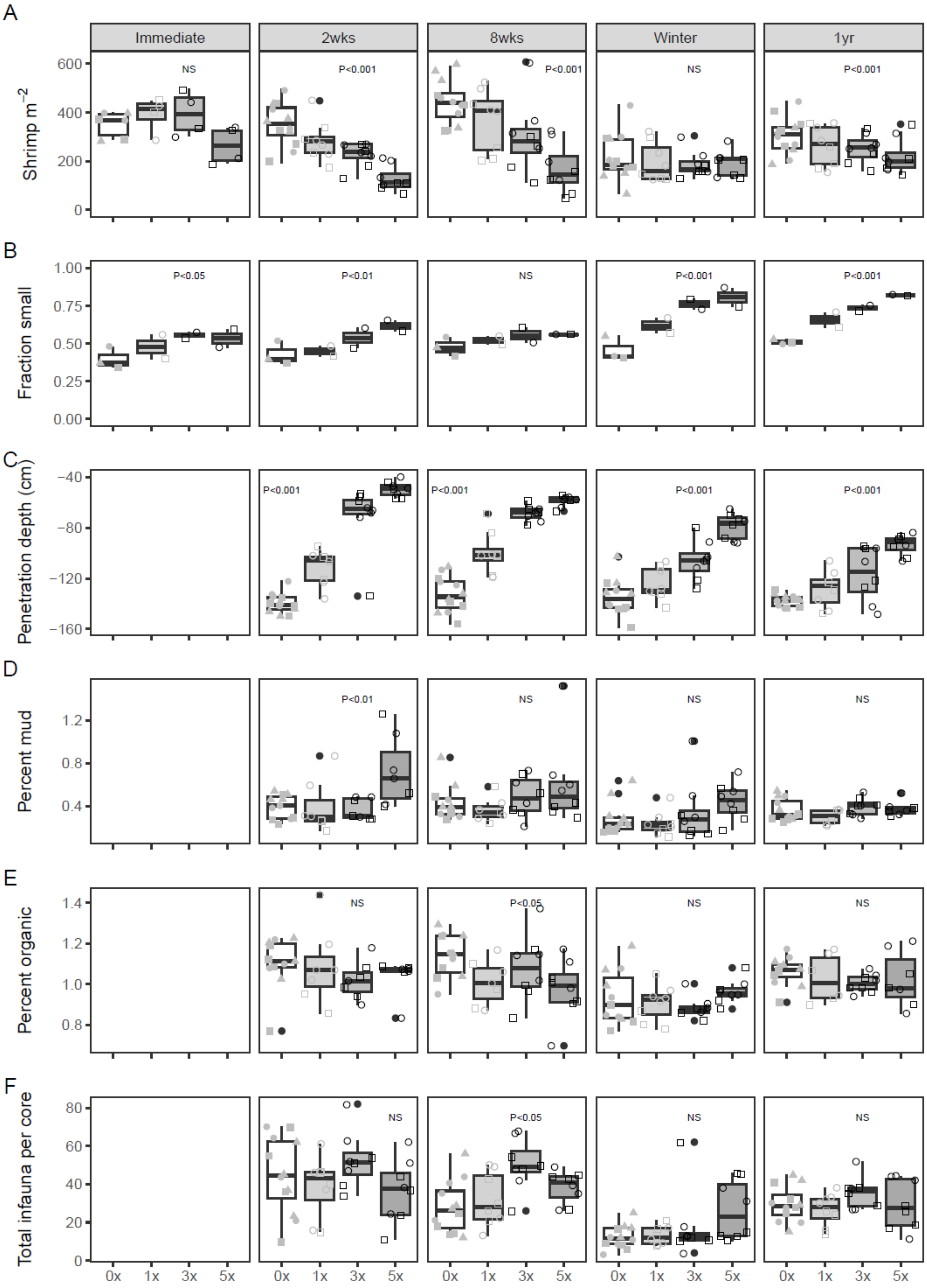
A
Immediate
2wks
8wks
Winter
1yr
Shrimp m^{-2}
600
400
200
0
NS
P<0.001
P<0.001
NS
P<0.001
B
Fraction small
1.00
0.75
0.50
0.25
0.00
P<0.05
P<0.01
NS
P<0.001
P<0.001
C
Penetration depth (cm)
−40
−80
−120
−160
P<0.001
P<0.001
P<0.001
P<0.001
D
Percent mud
1.2
0.8
0.4
P<0.01
NS
NS
NS
E
Percent organic
1.4
1.2
1.0
0.8
NS
P<0.05
NS
NS
F
Total infauna per core
80
60
40
20
0
NS
P<0.05
NS
NS
0x
1x
3x
5x

Figure 4. Responses to compaction of intertidal flats at Westport (Grays Harbor), Washington (USA) over one year following a gradient of compaction passes (1x, 3x, 5x) set up on 24 Jul 2024. A) Density of ghost shrimp *Neotrypaea californiensis* from core samples. B) Fraction of 1+-year old shrimp in small or extra-small size classes (>4 - <12.5 mm CL). C) Depth of penetration of a standard metal rod (negative is further into the ground). D) Percent mud (grain size <63 μm) in mineral sediment. E) Percent organic in dry sediment. F) Macro-infauna counts per core (diameter 10 cm, depth 10 cm). Immediate samples were collected one day after compaction, and each additional faceted column is a subsequent sample timepoint. Sampling occurred on two (0.16-ha) compacted beds at each compaction level (1x, 3x, 5x) interspersed between three reference beds; in the graphs, all subsamples from a bed share a point symbol. Boxplots are based on subsamples for visualization, but statistical analyses appropriately accounted for the nested design and true replicates of two compacted and three reference beds.

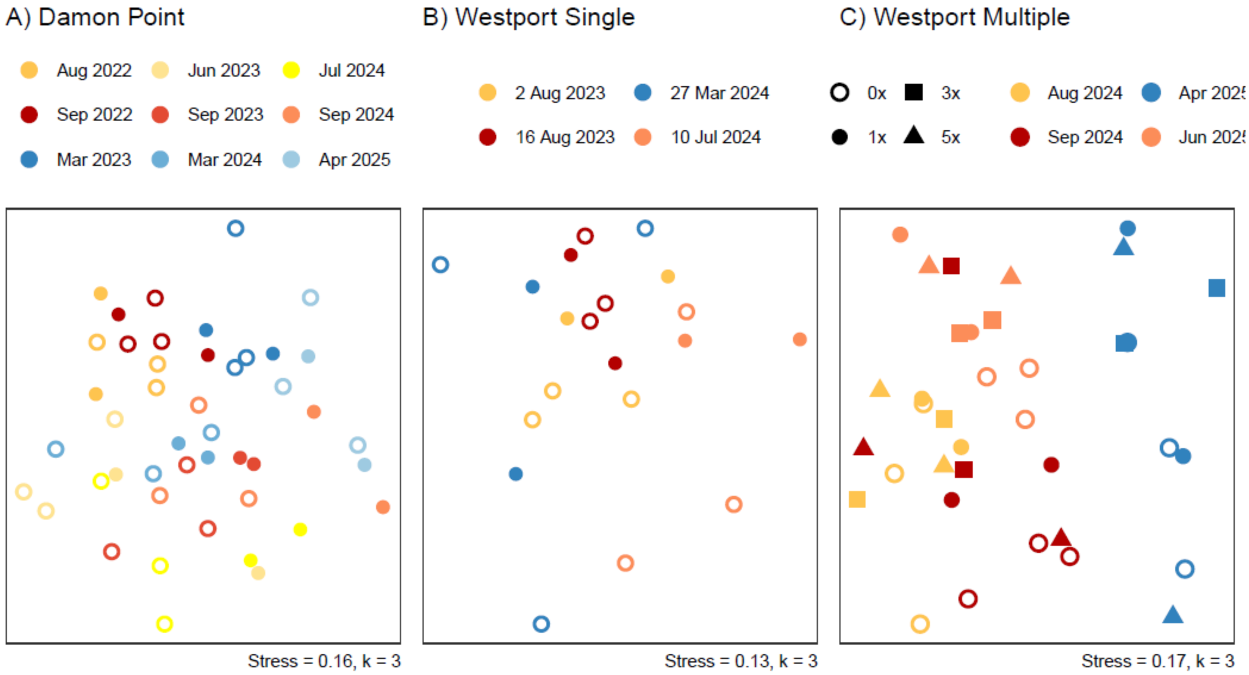

Figure 5. Infaunal communities from cores (diameter 10 cm, depth 10 cm) in compacted and reference beds, sieved to 0.5 mm and visualized by non-metric multidimensional scaling (excluding meiofauna, insects, and *Neotrypaea californiensis*). A) Damon Point, which was compacted in Aug 2022 and May 2023. B) Westport single-pass compacted in Aug 2023. C) Westport multiple-pass (1x, 3x, 5x) compacted in Jul 2024. Dates are distinguished by color and treatment by symbol. Subsamples within beds were averaged prior to calculation of Bray-Curtis dissimilarities, so symbols show each replicate bed.

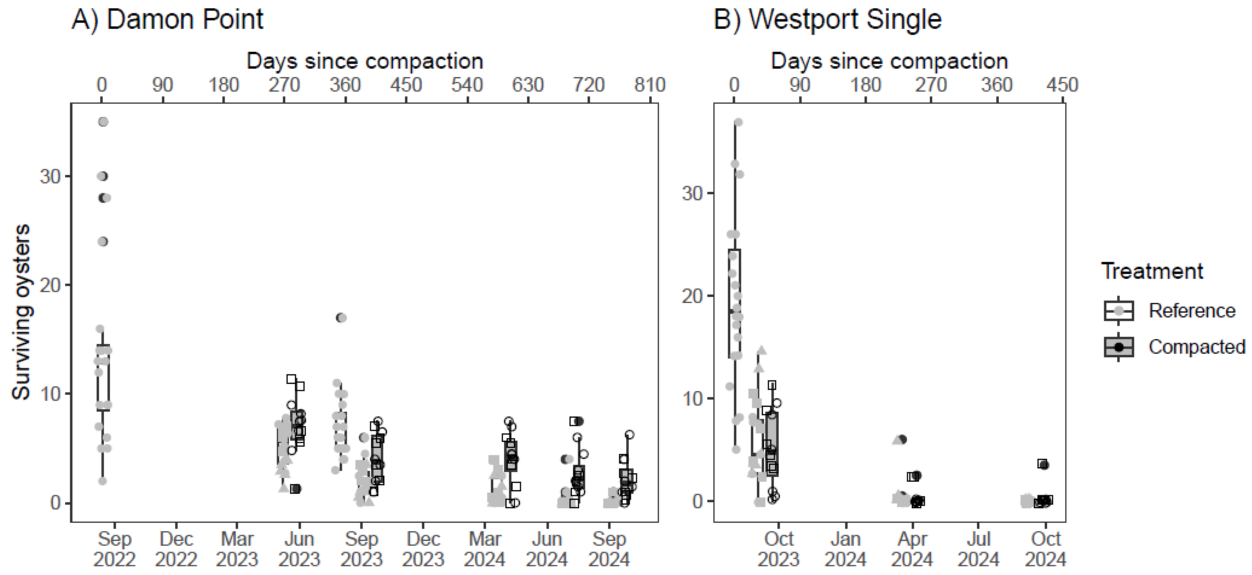

Figure 6. Survival of outplanted oysters (*Magallana gigas*) based on live oysters per tethered cultch in Grays Harbor, Washington (USA) following compaction treatments. A) Damon Point, which was compacted in Aug 2022 and again in May 2023. B) Westport single-pass, which was compacted in Aug 2023. Boxplots at dates with only reference values are initial counts on outplanted cultch. At other dates, reference and compacted values are offset by 20 days for clarity, although they were collected on the same day. Boxplots are based on subsamples within beds, averaging counts per cultch when multiple cultch were collected at a station; points with the same symbol are from the same bed. Statistical analyses appropriately accounted for the nested design and true replicates of two compacted and three reference beds.

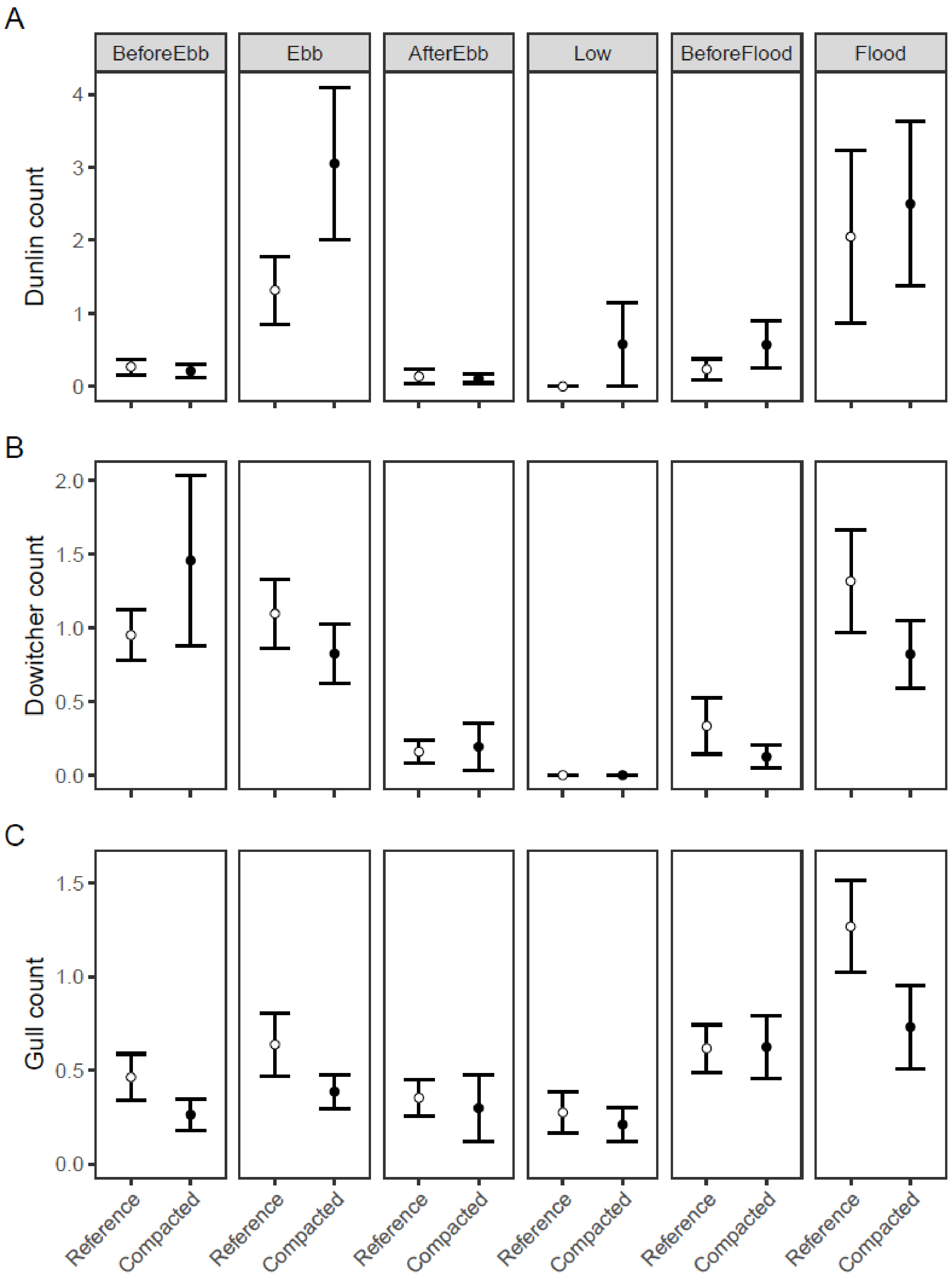
A
BeforeEbb
Ebb
AfterEbb
Low
BeforeFlood
Flood
Dunlin count
0
1
2
3
4
B
Dowitcher count
0.0
0.5
1.0
1.5
2.0
C
Gull count
0.0
0.5
1.0
1.5
Reference
Compacted

Figure 7. Counts of waterbirds by tidal stage from time-lapse photographs in April 2023 and 2024 at Damon Point (Grays Harbor), Washington (USA). A) Dunlin (*Calidris alpina*). B) Dowitchers (*Limnodromus* spp.). C) Gulls (*Larus* spp.). Each camera deployment resulted in eight photographs for each tidal stage, which were summed to generate subsamples. Points show mean values and error bars show standard error across all camera deployments on reference and compacted beds. Most beds had 25 camera deployments over two years, therefore about 50 subsamples contribute to compacted data and 75 subsamples contribute to reference data. Mean ± standard error were selected for visualization due to the very high frequency of zero counts (i.e. medians were zero at all stages). Statistical analyses appropriately accounted for the nested design, true replicates of two compacted and three reference beds across two years, and zero-inflated data.